Primary Productivity in Budd Inlet During 1997: Seasonal Patterns of Variation and Controlling Factors

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Introduction

The factors controlling the magnitude of primary production in a particular water column are complex, hence to understand and difficult to discriminate. Because primary productivity represents the product of m and B, where m is the specific growth rate (d^{-1}) and B is the biomass of the phytoplankton population (mg m^{-3}), a high primary production can be driven by either or both terms. The complexity arises because these terms in turn depend on both growth factors, such as solar radiation, dissolved nutrients, water temperature, as well as loss factors, such as grazing by zooplankton, mixing, and sinking within the water column. Thus, low primary production could be driven by low growth rates or from high loss rates to the biomass, just as high production can be driven by high growth rates or by a very large but slowly growing population.

We did not measure immediately. In order to quantify the specific growth rate of phytoplankton, and thus, if growth seems limited or not, one can calculate the P:B ratio (production/biomass). Phytoplankton production is measured in carbon units whereas phytoplankton biomass is measured via chlorophyll *a*. Unfortunately, the bias introduced to the P:B ratio from the variation in the C:chl (carbon/chlorophyll) conversion ratio can be substantial. Chlorophyll *a*, while in all phytoplankton, can vary widely in terms of its cellular quota due to photoadaptation, nutrient availability and other factors. In temperate waters where light changes dramatically with season and with depth, photo-adaptation can cause the chlorophyll per cell to vary widely, easily by a factor of four or more (Newton and Morello, 1998). This variability in chlorophyll per cell can dramatically bias estimates of the specific growth rates from the P:B ratio. Therefore, the P:B ratios presented here may not be indicating differences in growth, but rather, differences in cellular chlorophyll content.

Methods

Primary production was determined from the uptake of ^{14}C sodium bicarbonate in water samples drawn from Budd Inlet. Experiments were conducted at four stations, representing the three Inlet segments: BI-5 in the Inner Inlet; Loon-1 and BA-2 in the Central Inlet; and BD-2 in the Outer Inlet (Figure 1). The four sampling stations were visited approximately every three weeks during 1997 (Table 1), from January through October. Only stations BI-5 and Loon-1 were occupied until April, after which all four stations were sampled.

At each station, water samples were collected in Niskin bottles from six different light levels, corresponding to 100%, 50%, 25%, 12.5%, 6.25%, and 1.6% of surface light. The depth of the euphotic zone and these light levels were determined with a Secchi disk using standard techniques (Parsons et al., 1984), deriving the light extinction coefficient (k, in m^{-1}) for Puget Sound waters (Newton et al., 1997) as:

$$k = 1.6/\text{Secchi disk depth.} \quad (2)$$

From each light level, chlorophyll *a*, nutrients, and primary productivity (replicate light bottles and one dark bottle) were sampled. Replicate profiles of productivity bottles were filled, one for the ambient treatment and one for the nutrient spike treatment. For the nutrient spike, we added an initial concentration of 10 mM nitrogen (NH_4Cl) and 1 μM phosphorus (KH_2PO_4) to the seawater. To monitor nutrients over the course of the experiment, extra surface bottles were filled and sampled at 0 hr and 24 hr for nitrate, nitrite, ammonium, orthophosphate, and silicate.

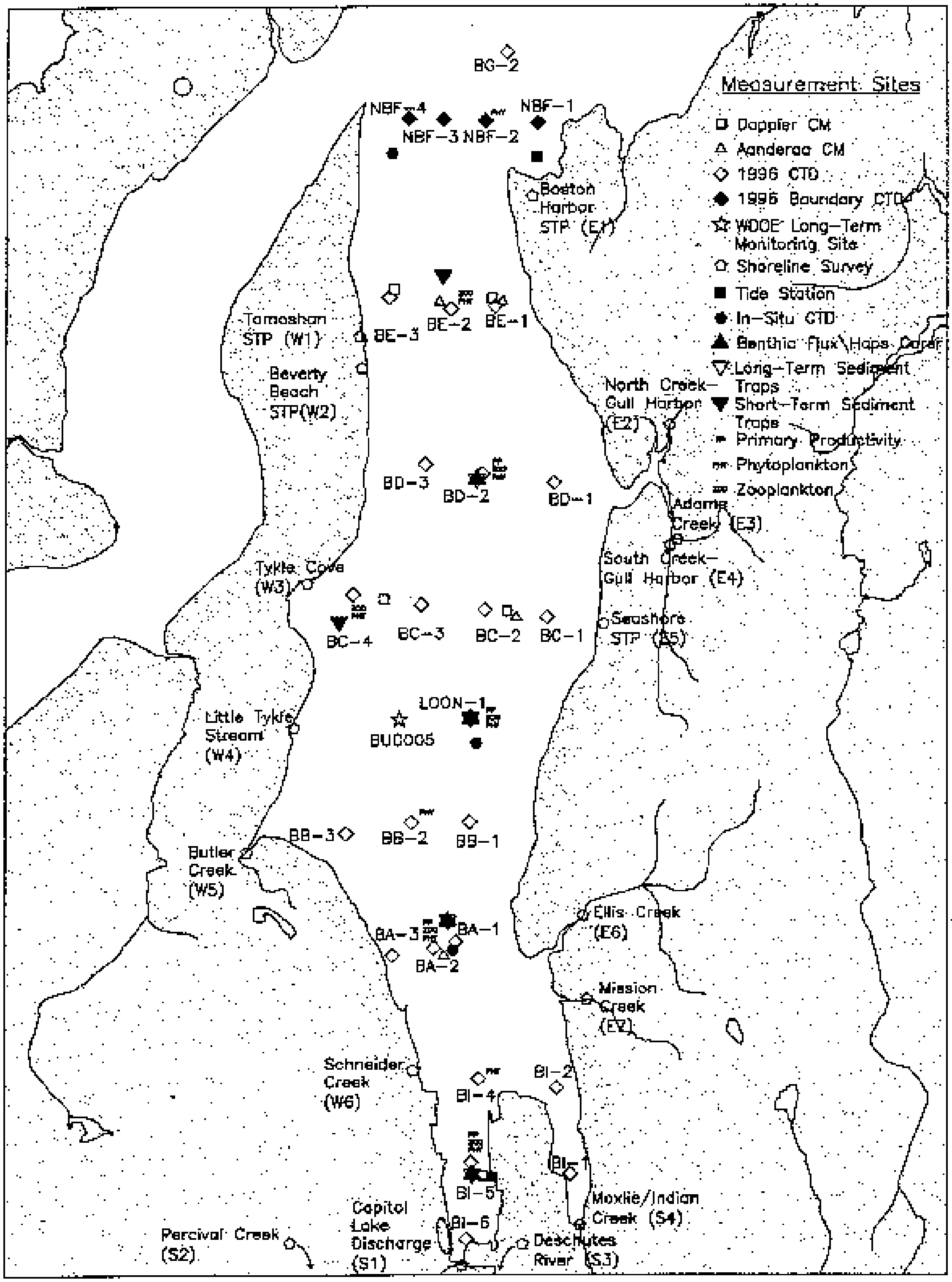

Figure 1. Map of stations and segments in Budd Inlet.

Table 1. Dates and station locations for primary production experiments in Budd Inlet.

		Stations			
		BI-5	**BA-2**	**Loon-1**	**BD-2**
		47 03.09 N	47 04.32 N	47 05.52 N	47 06.87 N
Experiment #	**Date**	122 54.27 W	122 54.65 W	122 54.53 W	122 54.72 W
1	16-Jan-97	X		X	
2	23-Jan-97	X		X	
3	27-Feb-97	X		X	
4	20-Mar-97	X		X	
5	3-Apr-97	X	X	X	X
6	22-Apr-97	X		X	
7	5-May-97	X	X	X	X
8	19-May-97	X	X	X	X
9	12-Jun-97	X	X	X	X
10	30-Jun-97	X	X	X	X
11	14-Jul-97	X	X	X	X
12	4-Aug-97	X	X	X	X
13	18-Aug-97	X	X	X	X
14	11-Sep-97	X	X	X	X
15	25-Sep-97	X	X	X	X

We incubated the primary productivity samples for 24 hr under simulated *in-situ* conditions using an outdoor tank plumbed with running seawater at West Bay Marina, Budd Inlet. Prior to the incubation, each primary productivity bottle was inoculated with ^{14}C-labeled sodium bicarbonate and, if appropriate the nutrient spike, and then placed in screen bags to simulate the light level from which it was collected. After 24 hr, the bottles were filtered onto glass fiber filters (Whatman, GF/F, normal pore size 0.7m) and the filters placed in vials with EcoLume scintillation cocktail. The specific activity of the filtered particulates was measured in a Beckman scintillation counter. Primary production was calculated as mg C m^{-3} d^{-1} using the basic equations found in Parsons et al. (1984), subtracting dark bottle DPMs from light bottle DPMs. Chlorophyll and nutrient samples were analyzed as previously described (Cox et al., this volume).

Results and Discussion

We present the patterns observed in the data collected during January–September of 1997 at 2–3 week intervals. Interpretations of these data must be made with strong caution due to two important caveats: 1) phytoplankton populations are highly variable on time scales much shorter than two weeks (i.e., days), thus we may have missed much of the variation; and 2) interannual variation has been observed to be quite strong in Budd Inlet, thus the representativeness of 1997 data is not known. During Department of Ecology's bi-weekly monitoring study in 1992–1994, the maximal integrated chlorophyll concentrations found at inner Budd Inlet monitoring stations during the years 1992, 1993, and 1994 were 155, 70, and 220 mg m^{-2}, respectively, and these maxima were observed in September, June, and July, respectively (Eisner and Newton, 1997).

Seasonal Variation

A distinct seasonal pattern was evident in the ambient primary production that is consistent with a temperate location (Figure 2). There was lower production in winter with higher production occurring from May through the end of September. Often at temperate latitudes a pattern of spring and fall blooms with reduced production in summer is observed. However, in Budd Inlet primary production remained high throughout the summer. Phytoplankton biomass, as indicated by chlorophyll *a*, also showed a seasonal pattern but it was somewhat different than that of primary production. There were distinct maxima in early May and the period of mid-July through early September, with reduced abundance in late May through early July (Figure 2). However, since phytoplankton populations can change very rapidly (within a day or two), we could be missing much in terms of the seasonal dynamics.

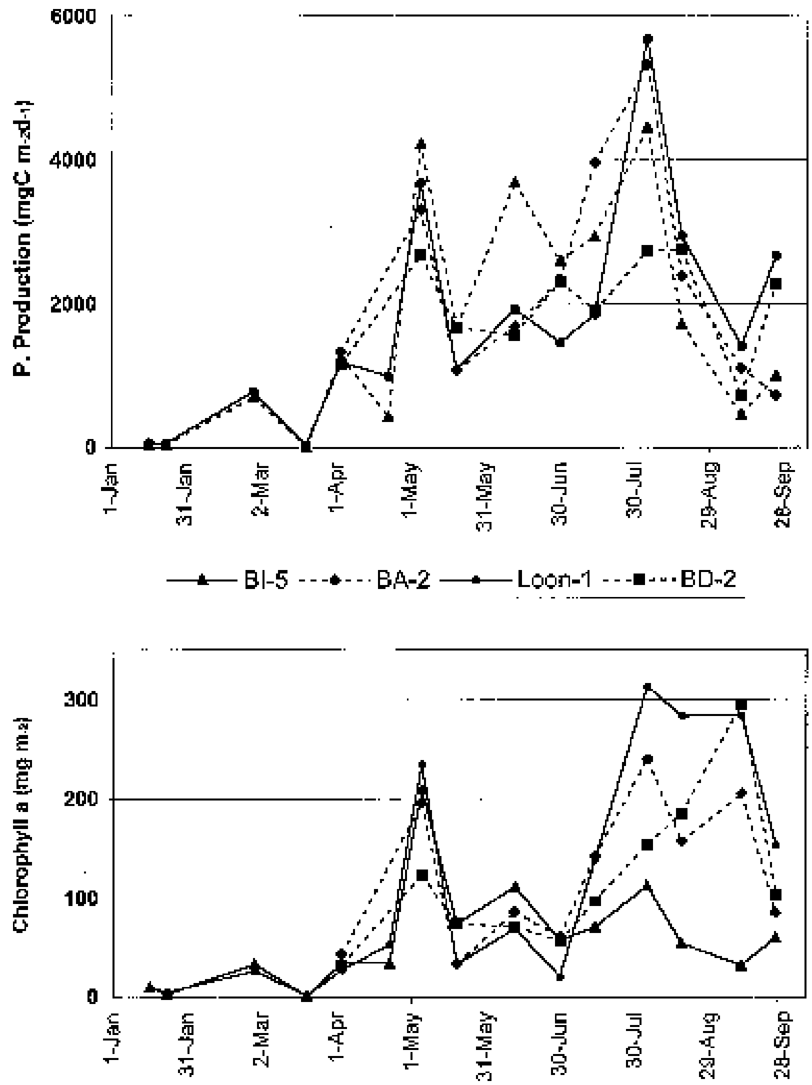

Figure 2. Seasonal pattern of primary production and phytoplankton biomass, as indicated by chlorophyll a. Values are integrated over the euphotic zone.

The P:B ratios calculated in Table 2 show highest values during April through August. This reflects an expected increase in growth rate during the temperate growing season. Photoadaptation to high light in summer can bias P:B ratios to be too high, just as low light adaptation can result in low P:B ratios.

Table 2. Primary productivity and water column conditions in Budd Inlet during 1997. Integrated variables are integrated over the euphotic zone.

Expt #	Date	Station	Integrated PP (mg C m^{-2} d^{-1})	Integrated chl (mg chl m^{-2})	P:B (mg C mg chl^{-1} d^{-1})	Euphotic zone (m)	Incident radiation (moles m^{-2} d^{-1})	Integrated DIN (mM m^{-1})
1	16-Jan-97	BI-5	46	10	5	11.2	2.39	383
		Loon-1	67	10	7	13.0	2.39	275
2	23-Jan-97	BI-5	32	3.4	9	5.5	12.8	162
		Loon-1	57	5.4	11	8.1	12.8	245
3	27-Feb-97	BI-5	700	33	21	13.0	21.7	408
		Loon-1	779	26	30	14.4	21.7	335
4	20-Mar-97	BI-5	6	1.1	5	1.7	32.6	31
		Loon-1	29	2.0	15	2.3	32.6	47
5	3-Apr-97	BI-5	1255	35	36	12.1	40.7	302
		BA-2	1331	43	31	17.0	40.7	321
		Loon-1	1185	27	43	18.7	40.7	347
		BD-2	1155	33	35	17.0	40.7	242
6	22-Apr-97	BI-5	428	34	13	3.5	17.8	50
		Loon-1	996	53	19	4.3	17.8	43
7	5-May-97	BI-5	4235	209	20	5.8	18.4	15
		BA-2	3319	196	17	5.2	18.4	23
		Loon-1	3687	235	16	5.8	18.4	53
		BD-2	2678	124	22	5.0	18.4	55
8	19-May-97	BI-5	1662	74	22	12.2	36.7	1
		BA-2	1291	27	48	12.2	36.7	2
		Loon-1	1075	33	32	7.2	36.7	40
		BD-2	1345	39	34	8.6	36.7	0
9	12-Jun-97	BI-5	3692	111	33	4.6	34.9	0
		BA-2	1685	86	20	4.3	34.9	5
		Loon-1	1931	69	28	4.0	34.9	54
		BD-2	1565	71	22	3.6	34.9	6

Table 2 (continued). Primary productivity and water column conditions in Budd Inlet during 1997. Integrated variables are integrated over the euphotic zone.

Expt #	Date	Station	Integrated PP (mg C m^{-2} d^{-1})	Integrated chl (mg chl m^{-2})	P:B (mg C mg chl^{-1} d^{-1})	Euphotic zone (m)	Incident radiation (moles m^{-2} d^{-1})	Integrated DIN (mM m^{-1})
10	30-Jun-97	BI-5	2601	58	45	12.2	41.3	108
		BA-2	2342	61	38	11.5	41.3	177
		Loon-1	1459	21	70	16.5	41.3	161
		BD-2	2322	57	41	19.4	41.3	67
11	14-Jul-97	BI-5	2639	71	37	6.5	40.3	2
		BA-2	3963	142	28	5.0	40.3	10
		Loon-1	1856	139	13	5.0	40.3	76
		BD-2	1896	97	20	5.0	40.3	3
12	4-Aug-97	BI-5	4448	112	40	7.2	51.4	8
		BA-2	5325	240	22	8.6	51.4	17
		Loon-1	5679	314	18	8.6	51.4	17
		BD-2	2736	154	18	9.4	51.4	4
13	18-Aug-97	BI-5	1719	54	32	7.2	27.0	3
		BA-2	2394	156	15	7.2	27.0	66
		Loon-1	2951	283	10	10.1	27.0	33
		BD-2	2758	185	15	14.4	27.0	6
14	11-Sep-97	BI-5	446	32	14	15.8	21.1	6
		BA-2	1098	205	5	4.3	21.1	4
		Loon-1	1406	284	5	3.6	21.1	170
		BD-2	716	295	2	5.0	21.1	4
15	25-Sep-97	BI-5	996	60	17	7.9	18.4	61
		BA-2	715	85	8	5.8	18.4	124
		Loon-1	2676	153	17	8.6	18.4	161
		BD-2	2282	104	22	10.8	18.4	55

Budd Inlet is a highly productive location, even within Puget Sound. Despite its shallow depth, the integrated production approached 6000 mg C m^{-3} d^{-1} (Figure 2). Another regional bay that has been well studied is Dabob Bay, a northward offshoot of Hood Canal (Downs and Lorenzen, 1985 and references within). The maximum primary production observed in an annual cycle during the years 1982–1985 ranged ~2000 to 4500 mg C m^{-3} d^{-1} (Downs, 1989). The water column at the sampling site in Dabob is 110 m deep whereas Budd Inlet stations average only 10 m. Often the euphotic zone extended beyond the sea–bed in Budd Inlet (Figure 3) meaning that sufficient light for photsynthesis was available to the entire water column. Phytoplankton biomass, as indicated by chlorophyll *a* integrated over the euphotic zone, was also comparatively high in Budd Inlet, with a seasonal maximum at just over 300 mg chl m^{-2} (Figure 2). Similar values for Dabob Bay for 1982–1985 ranged ~125 to 225 mg chl m^{-2}. The 1997 data are higher than that found in the Inner Inlet by Ecology during the 1992–1994 monitoring as previously mentioned in this section; however, values for the central Inlet (where the greatest population occurs) are not available, due to differences in sampling technique.

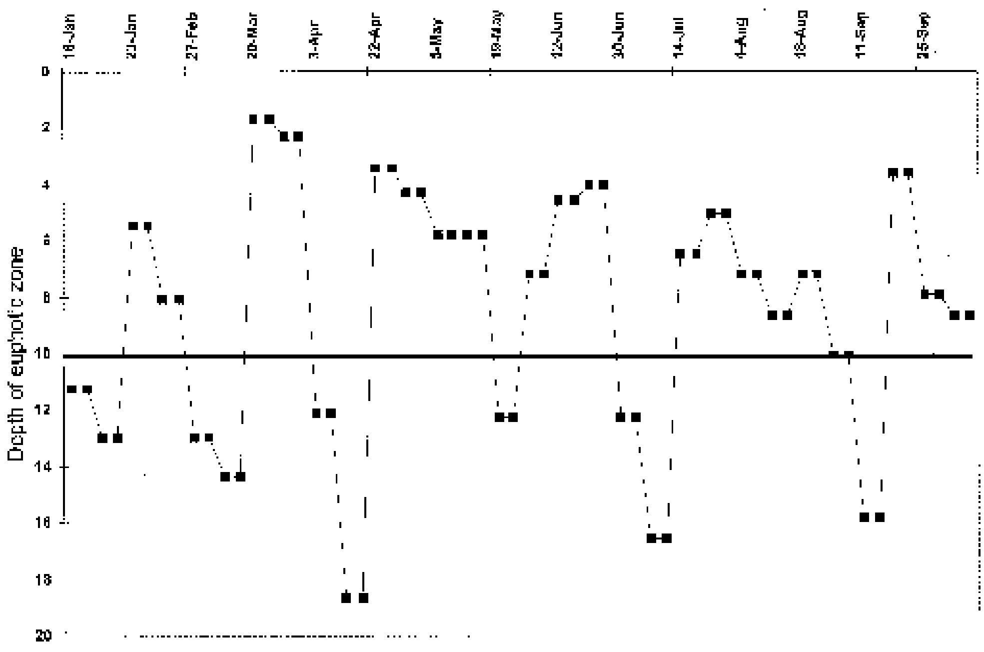

Figure 3. Depth of the euphotic zone (1% of surface radiation) at BI-5 and Loon-1 over the course of study. Seabed depth at these stations is 10 m.

Nutrients collected from the same bottles as the productivity samples showed a marked decline during the month of April (Figure 4) that inversely mirrored the increase in primary production. Based on these results, we conclude that for 1997, the spring bloom appeared to occur in April. However, strong variation in the timing of the spring bloom occurs regionally due to forcing by weather-related attributes. The timing of the spring bloom is driven by weather, both solar radiation and wind stress, as well as by hydrographic conditions and river input. For Dabob Bay during 1982–1985, the onset of the spring bloom ranged February through May. As stated, caution should be used when interpreting seasonal patterns based on the 1997 data alone. Monitoring of Budd Inlet by Ecology in 1992–1994 did not occur commence early enough in the year to make this assessment.

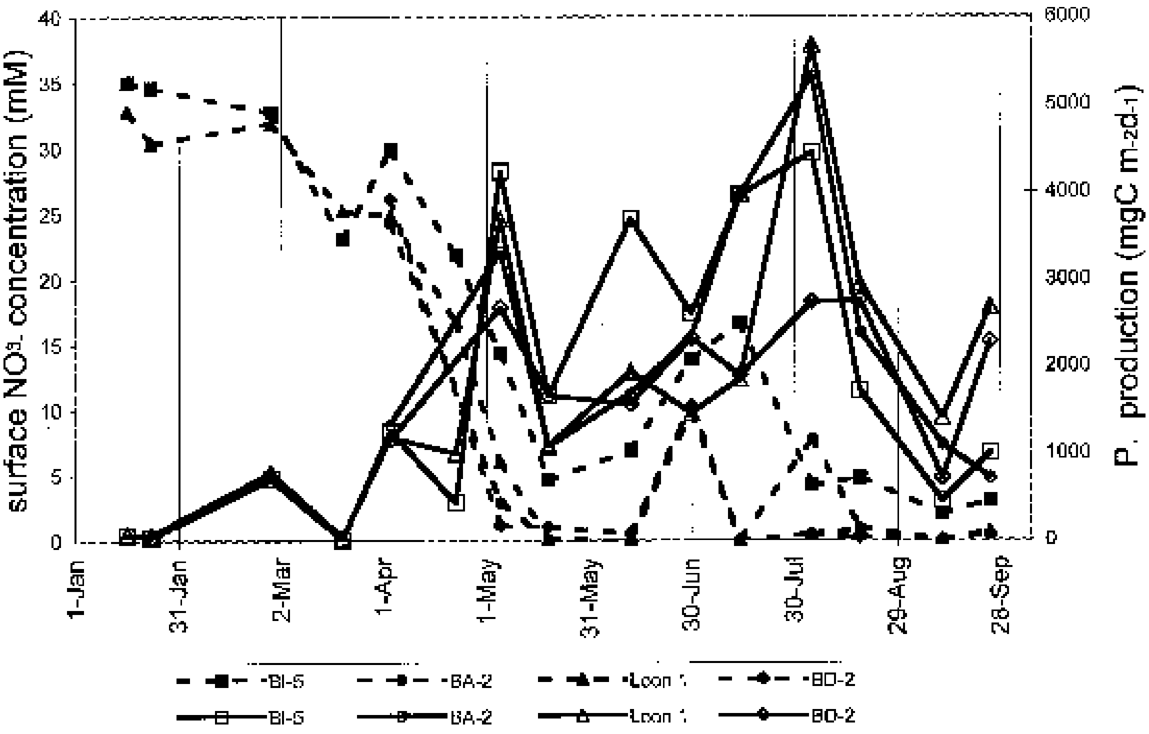

Figure 4. Seasonal plot of surface nitrate concentration (dotted lines) and primary production (solid lines) during 1997. Note that for all stations a marked decrease in nitrate in April–May is accompanied by an upswing in production; however, note caveat regarding interannual variation in text.

Spatial Variation

There was no strong or consistent pattern in spatial variation of production or biomass in Budd Inlet, however the central bay stations (BA-2 and Loon-1) often had the highest values for both (Table 2). A similar observation of the highest phytoplankton abundance being found in the central inlet was seen in Ecology's previous assessment of Budd Inlet chlorophyll (Eisner and Newton, 1997). It is possible that either a weak gyre in the observed circulation or tidal pumping concentrates phytoplankton in this area (Ebbesmeyer, this volume).

Comparing BI-5 and Loon-1, since we have full time records for these stations, we see that integrated primary production was higher at BI-5 than Loon-1 in early summer (June–July), whereas in late summer (August–Sept.) both integrated production and especially chlorophyll were much lower at BI-5 than at Loon-1 (Figure 5). Looking at the other stations (Figure 2), we see that BI-5 had much lower chlorophyll than all stations during late summer. The mechanism for this pattern is not entirely clear. Despite the lower biomass in late summer, BI-5 production remained relatively high.

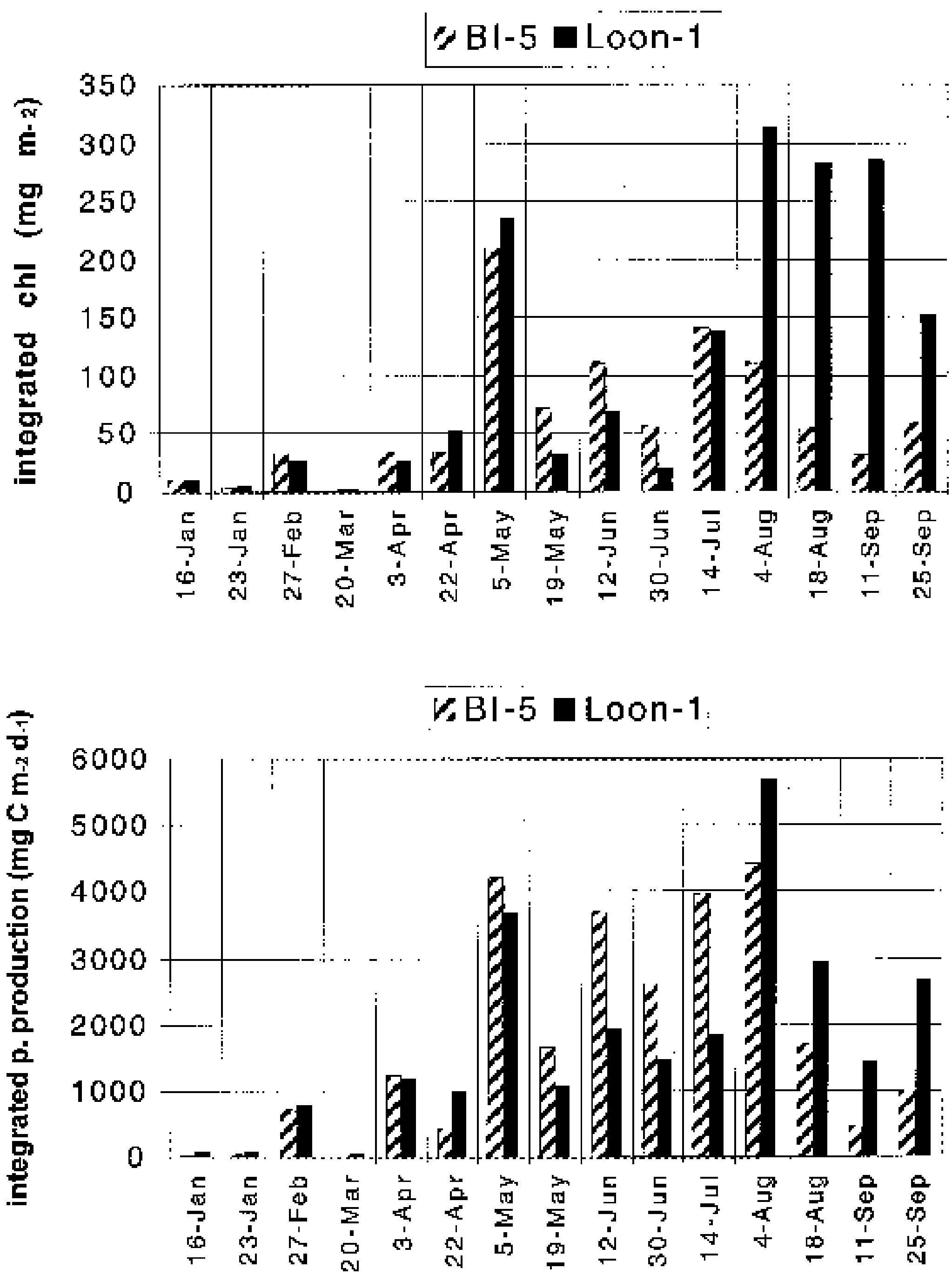

Figure 5. Seasonal values of integrated chlorophyll and primary production at BI-5 and Loon-1.

Nutrient data from at the productivity depths showed that the Inner Inlet (BI-5) had the highest surface nitrate and ammonium concentrations (Figures 6–7). Exceptionally high ammonium concentrations were found throughout the water column at BI-5, especially at depth where concentrations from May through July were 6–20 times higher than at any other station. The role of nitrogenous nutrient release from the sediments in the annual cycle and implications for flushing at this Inner Inlet station must both be regarded seriously in light of this strong signal.

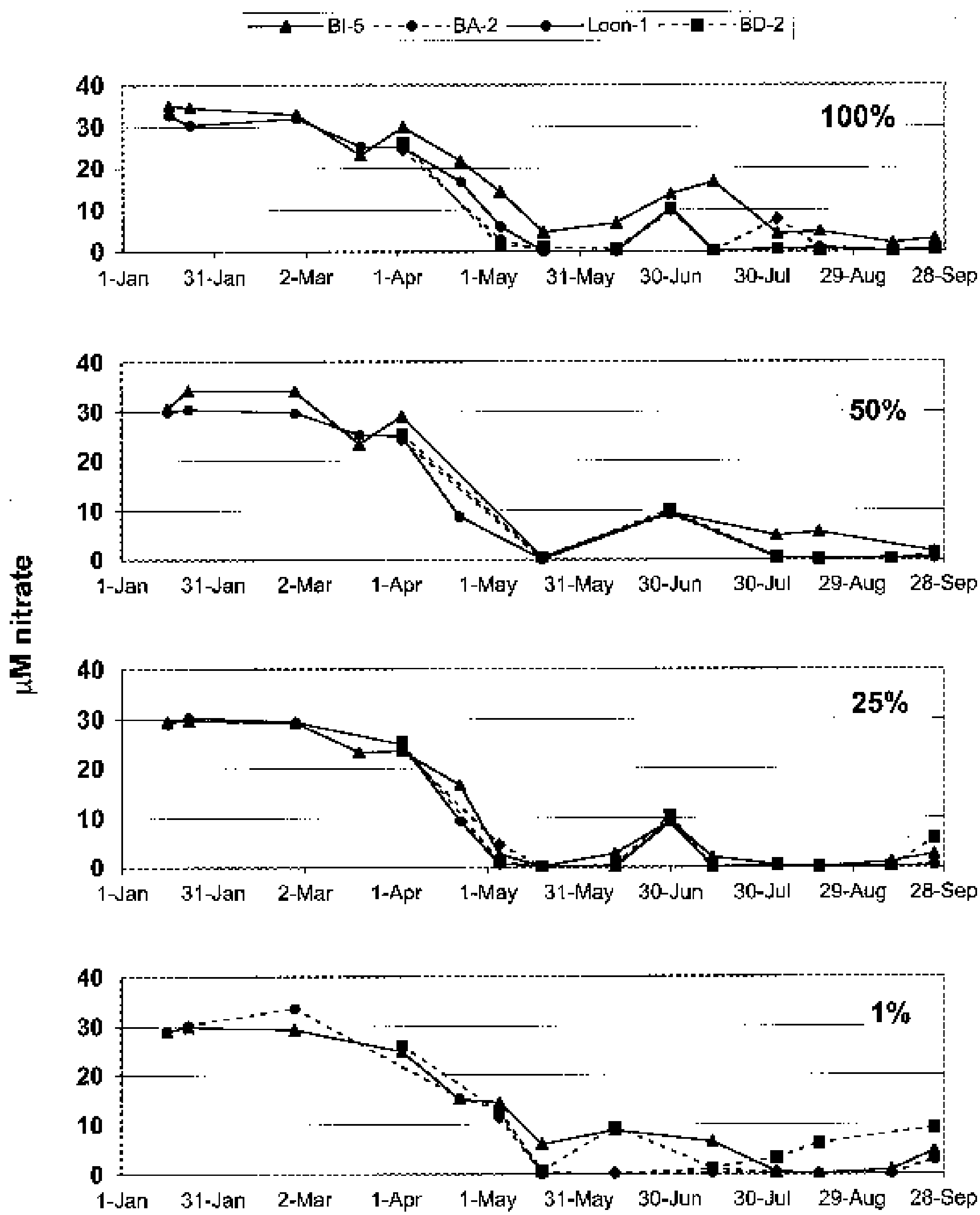

Figure 6. Ambient concentrations of nitrate (mM) at the depths of the various light levels as indicated.

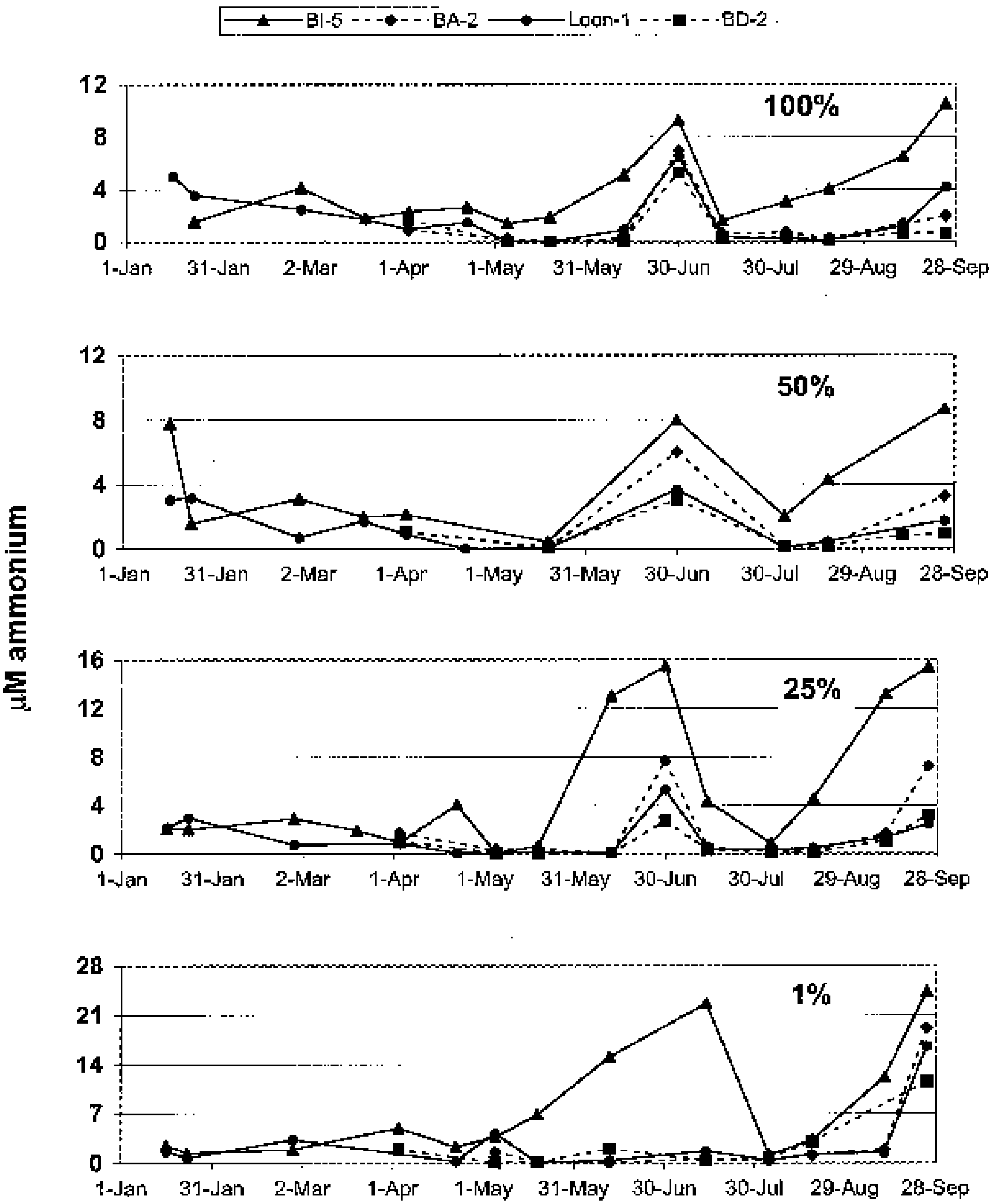

Figure 7. Ambient concentrations of ammonium (mM) at the depths of the various light levels as indicated.

Controls on Ambient Production

A shift from low production to higher production occurred in April 1997. The lower production period encompasses the first five experiments. Based on the nutrient and production data, all the remaining experiments have a similar character (Figure 4); however the chlorophyll data show the last four experiments to have distinctly high values (Figure 2). We thus compartmentalized the data into these three bins (experiments 1–5, 6–11, and 12–15) to look for patterns in the correlation of production with possible controlling growth factors such as light, nutrients and biomass. Other factors, such as temperature and water column stability undoubtedly influence growth.

Phytoplankton biomass is one of the determinants of primary production (equation 1) so we would expect fairly strong correlations to be evident. For the first five experiments (Jan–Apr), we see a strong correlation (Figure 8a) that decreases but is still significant for all the experiments (Figure 9a). The most variation comes from the later experiments (Aug–Sept) and some of this may be due to variation in C:chl ratios.

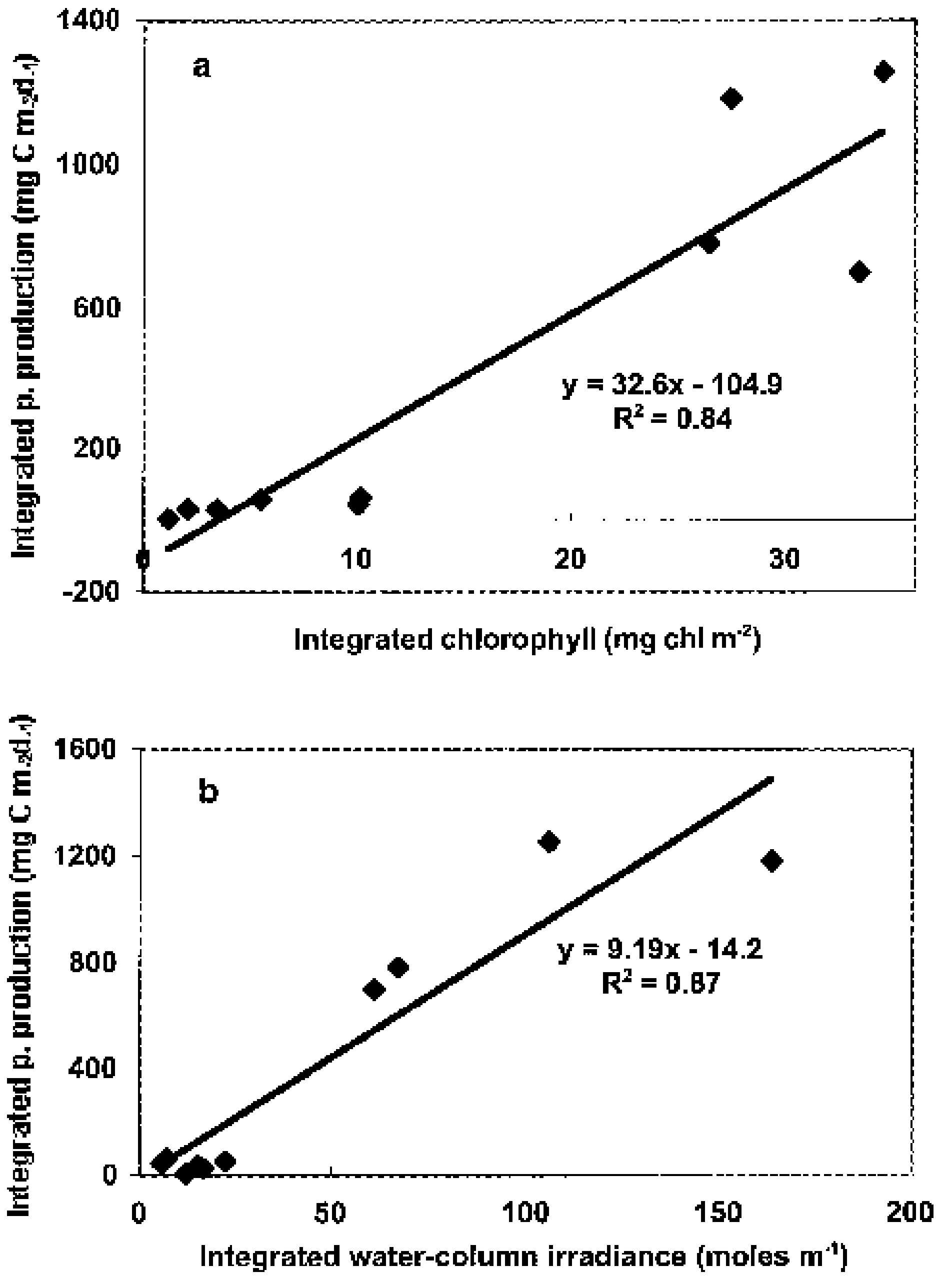

Figure 8. Correlation of integrated primary production with chlorophyll (A) and water column irradiance (B) for first five experiments (Jan–Apr, 1997) at BI-5 and Loon-1.

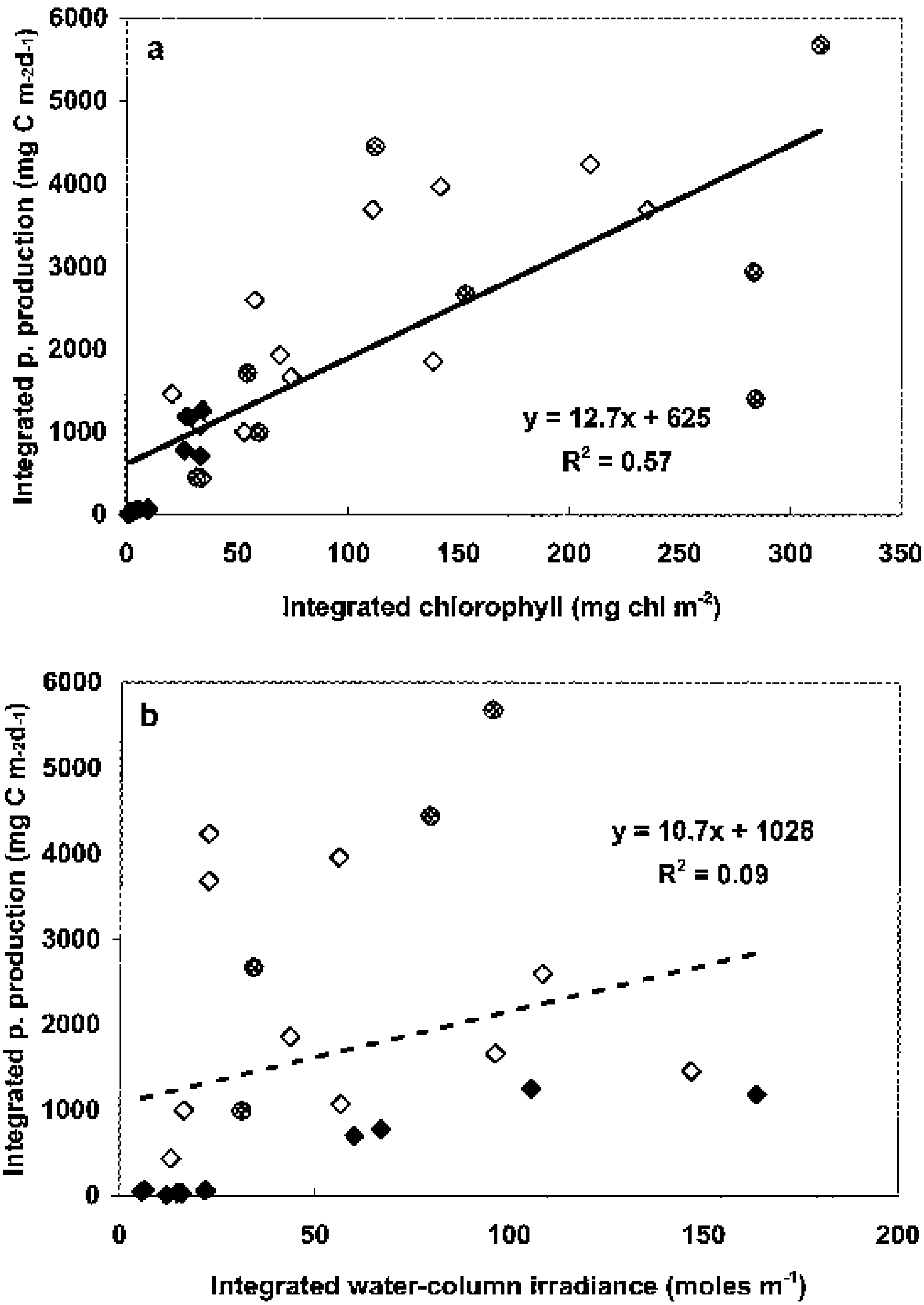

Figure 9. Correlation of integrated primary production with chlorophyll (A) and water column irradiance (B) for all 1997 experiments at BI-5 and Loon-1. Dark diamonds = 1–5; open diamonds = expts 6–11; grey diamonds = expts 12–15.

Light available to phytoplankton is a function of the level of incoming solar radiation as well as how much particulate material there is in the water column that will attenuate the light. The particulate material may be either sediment or biogenic (e.g., phytoplankton cells). To account for this in our evaluation of light control on primary production, we calculated the light integrated within the euphotic zone. Primary production was strongly correlated with euphotic zone light during the early experiments (Figure 8b). As the year progressed, this relation weakened to a non-significant level (Figure 9b), indicating that other factors were exerting primary control on production.

Nitrogenous nutrients were in short supply (Table 2, Figures 6 and 7) during much of the growth season. It is difficult to interpret nitrogen control of growth based on ambient nutrient concentrations since concentrations cannot reflect uptake rates but, rather, the net balance of supply and uptake. To assess nutrient control of phytoplankton growth we added nutrient spikes; these results are discussed below and show that nutrients play a vital role in controlling growth, especially from May through September.

Effect of Nutrient Addition

If light appears to exert the primary control production during the Jan–April time period, then what effect would nutrients have on ambient production at that time? This was assessed using the nutrient spike results.

As shown in Figure 10, the addition of nutrients had a strong positive effect on production for the experiments from May through August. However, since ambient production is so much lower before May, an expanded scale is necessary to view the wintertime results. As shown in Figure 11, there were two instances of increased production during the Jan–April time period. Taken as a percentage, ambient production increased by 10–39% in this time period (Figure 12). This increase pales in comparison with the up to 80% increases noted in June–July. However, at issue is the quantity of carbon produced from N-fertilization and what this could mean to the oxygen debt in the bottom waters of Budd Inlet.

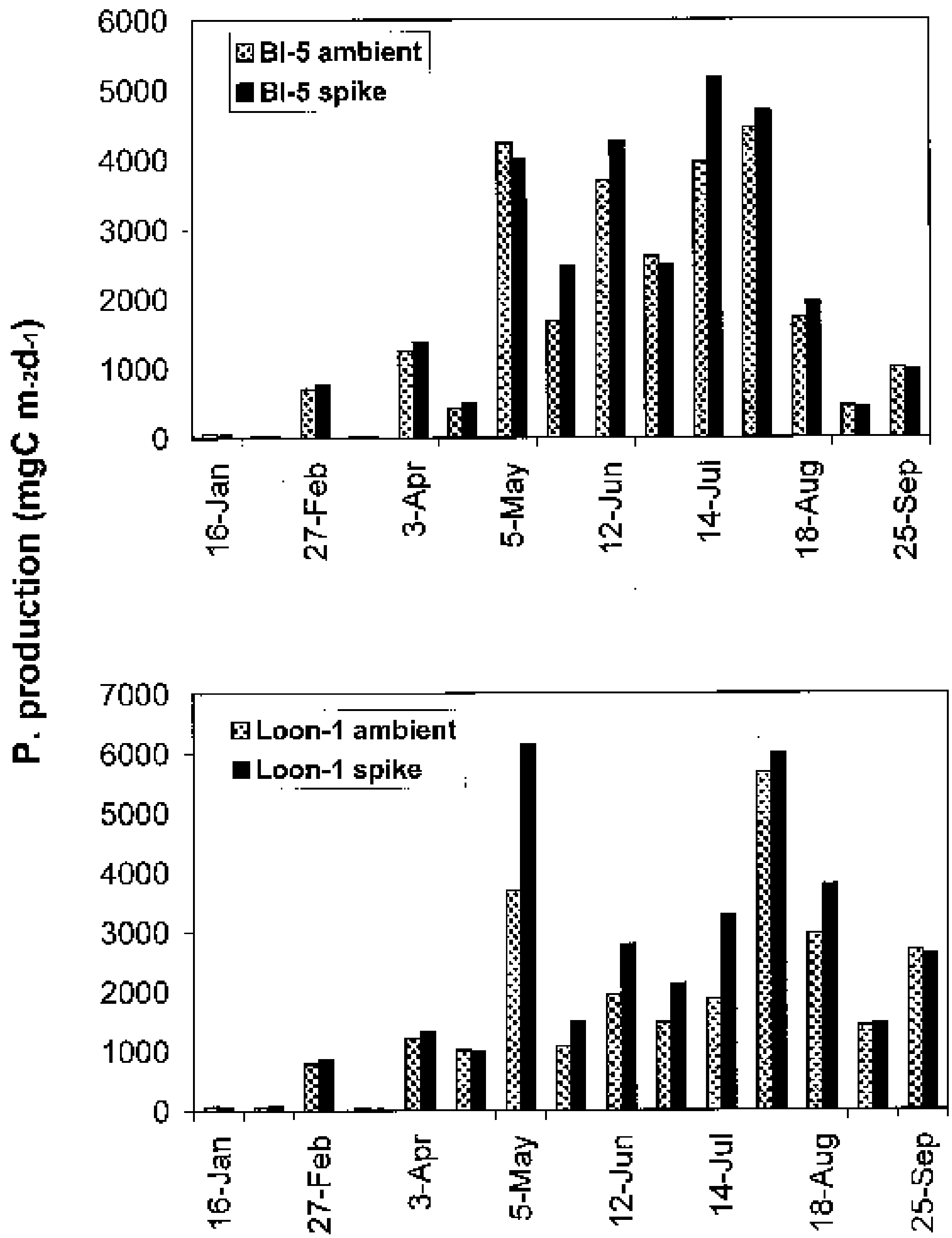

Figure 10. Effect of added nutrient spike on ambient primary production in Budd Inlet.

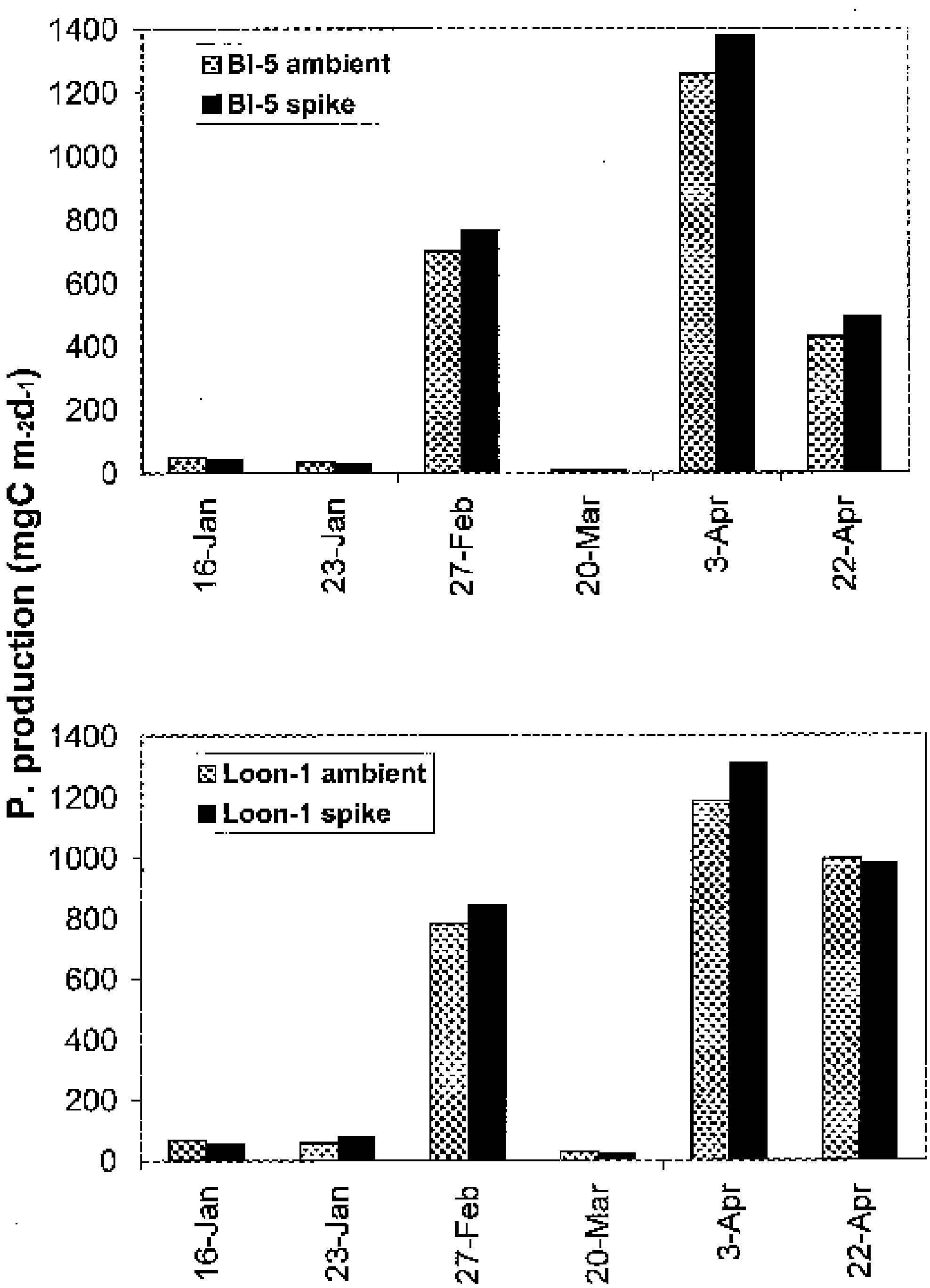

Figure 11. Effect of added nutrient spike on ambient primary production in Budd Inlet in winter and early spring.

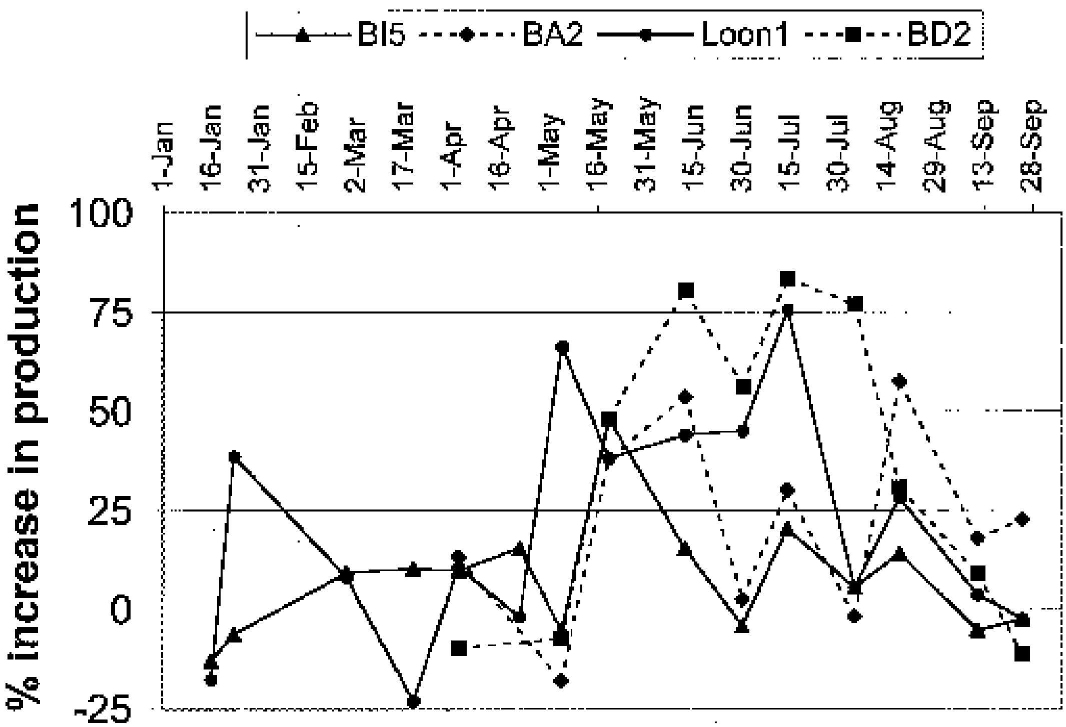

Figure 12. The percent increase in ambient primary production found in the treatment with nutrient spike addition.

The individual values for these experiments are listed in Table 3. The observed winter–spring increases ranged 63–174 mg C m^{-3} d^{-1}. The method has a precision of at least 20 mg C m^{-3} d^{-1}. Increases greater than 30 mg C m^{-3} d^{-1} are likely to be above experimental noise. There are times when the nutrient spike treatment produced less carbon than the ambient and this was, interestingly, most prevalent in the surface samples of BI-5. A mechanism for this result is not known.

The production increases were recorded on sunny days (27 Feb 97 and 3 Apr 97), as would be expected since we observe production to be highly correlated with solar radiation. In one case (20 Mar 97) there was high incident radiation, but strong runoff with high amounts of suspended sediments reduced water transparency substantially. In most cases, however, we could expect that increased production could be sustained for the period of a crisp, clear, sunny weather pattern that often occurs in our region in winter/early spring.

In order to help assess the impact of adding nutrients to Budd Inlet in wintertime, the duration of sunny wintertime weather patterns should be determined. Then, the maximum carbon production increases as indicated by this study (i.e., 50–200 mg C m^{-3} d^{-1}) should be scaled to the duration of sunny wintertime weather patterns. This carbon quantity should be modeled within the system to reflect the reduction of oxygen concentration in order to investigate water quality effects (lowering of DO by >0.2 mg/L) to inner Budd Inlet.

Table 3. Effect of nutrient spike on primary production obtained from Budd Inlet. Bold indicates production change greater than 30 mg C m^{-2} d^{-1} or than 25%.

Expt #	Date	Station	Ambient integrated PP (mg C m^{-2} d^{-1})	Spiked integrated PP (mg C m^{-2} d^{-1})	Delta production (mg C m^{-2} d^{-1})	% change
1	16-Jan-97	BI-5	46	40	-6	-13
		Loon-1	67	55	-12	-18
2	23-Jan-97	BI-5	32	30	-2	-6
		Loon-1	57	79	22	**39**
3	27-Feb-97	BI-5	700	764	**64**	9
		Loon-1	779	842	**63**	8
4	20-Mar-97	BI-5	6	6	0	7
		Loon-1	29	22	-7	-23
5	3-Apr-97	BI-5	1255	1376	**121**	10
		BA-2	1331	1505	**174**	13
		Loon-1	1185	1311	**126**	11
		BD-2	1155	1041	**-114**	-10
6	22-Apr-97	BI-5	428	494	**66**	15
		Loon-1	996	977	-19	-2
7	5-May-97	BI-5	4235	4012	**-223**	-5
		BA-2	3319	2717	**-603**	-18
		Loon-1	3687	6132	**2445**	**66**
		BD-2	2678	2481	**-197**	-7
8	19-May-97	BI-5	1662	2461	**799**	**48**
		BA-2	1291	1502	**211**	16
		Loon-1	1075	1485	**410**	**38**
		BD-2	1345	1638	**293**	22
9	12-Jun-97	BI-5	3692	4255	**563**	15
		BA-2	1685	2588	**903**	**54**
		Loon-1	1931	2782	**851**	**44**
		BD-2	1565	2821	**1256**	**80**
10	30-Jun-97	BI-5	2601	2492	**-109**	-4
		BA-2	2342	2399	**57**	2
		Loon-1	1459	2117	**658**	**45**
		BD-2	2322	3628	**1306**	**56**
11	14-Jul-97	BI-5	2639	3535	**896**	**34**
		BA-2	3963	5154	**1191**	**30**
		Loon-1	1856	3260	**1404**	**76**
		BD-2	1896	3476	**1580**	**83**
12	4-Aug-97	BI-5	4448	4693	**245**	6
		BA-2	5325	5228	**-97**	-2
		Loon-1	5679	5996	**317**	6
		BD-2	2736	4838	**2102**	**77**
13	18-Aug-97	BI-5	1719	1959	**240**	14
		BA-2	2394	3771	**1377**	**58**
		Loon-1	2951	3781	**830**	**28**
		BD-2	2758	3605	**847**	**31**
14	11-Sep-97	BI-5	446	422	-24	-5
		BA-2	1098	1295	**197**	18
		Loon-1	1406	1458	**52**	4
		BD-2	716	780	**64**	9
15	25-Sep-97	BI-5	996	970	-26	-3
		BA-2	715	877	**162**	23
		Loon-1	2676	2613	**-63**	-2
		BD-2	2282	2026	**-256**	-11

Other Important Considerations

The focus of the Budd Inlet Science Study was on quantifying carbon production from phytoplankton and following the cycles of nutrients and oxygen. However, it should be noted that qualitative changes to the phytoplankton community could be possible from added nutrient supply.

Little is known regarding what controls phytoplankton species composition and succession. Diatoms are the primary phytoplankton group in Budd Inlet throughout most of the year; however, dinoflagellates can be numerically dominant in summer (Eisner and Newton, 1997). Harmful forms of phytoplankton (*Pseudonitschia* spp. leading to amnesiac shellfish poisoning, *Heterosigma carterae* leading to fish kills, *Alexandrium catenella* leading to paralytic shellfish poisoning) have been observed in Budd Inlet (Eisner and Newton, 1997). The stimulus for a particular species to bloom is not known; however, nutrient dynamics are suspected in having a role in determining phytoplankton species succession (Justic et al., 1995; Conley and Malone, 1992; Hecky and Kilham, 1988; Officer and Ryther, 1980). The importance of such a mechanism during winter is not known, though it would likely be much lower than in summer.

One influencing factor on phytoplankton species shifts due to eutrophication has been the N:P (nitrogen/ phophoruss) ratio (refs). In nature, nitrogen and phosphorus are taken up by phytoplankton at a ratio of 16 to 1 (Redfield et al., 1963). When nutrients are added from anthropogenic sources, often the ratio is skewed significantly. This, in addition to the exact form of the nutrients (e.g., dissolved organic nitrogen vs. ammonium vs. nitrate) can be a determinant in phytoplankton species selection. Although the knowledge on this subject is incomplete and is difficult to obtain, additions of nutrients closer to the Redfield ratio of 16:1 would hold less risk of upsetting natural communities.

Summary of Observations

- Budd Inlet has very high primary productivity relative to other Puget Sound locations.
- A marked seasonal range in primary production was evident in 1997, but summertime lows were not seen.
- The highest production shifted from the Inner Inlet (May–June) to the mid-inlet (July–Sept), and this may be driven by patterns in biomass distribution.
- Light was a significant determinant of winter production levels.
- Added nutrients increased production year-round. Although the effect was smaller in winter, it was observed to be as high as a 35% increase.

References

Conley and Malone. 1992. Marine Ecological Progress Series, 81: 121–128.

Downs, J.N. 1989. Implications of the phaeopigment, carbon and nitrogen content of sinking particles for the origin of export production. Ph.D. dissertation, University Washington, 196 pp.

Downs, J.N. and C.J. Lorenzen. 1985. Carbon:pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. Limnol. Oceanogr. 30: 1024–1036.

Eisner, L.B. and J.A. Newton. 1997. Budd Inlet Focused Monitoring Report for 1992, 1993 and 1994. Washington State Department of Ecology, Environmental Investigations and Laboratory Services Program, Publication #97-327, Olympia, WA.

Hecky R.E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnology and Oceanography, 33: 796–822.

Justic, D., N.N. Rabalais, R.E. Turner, and Q. Dortch. 1995. Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. Estuarine, Coastal & Shelf Sci, 40: 339–356.

Newton, J.A., S.L. Albertson, and A.L. Thomson. 1997. Washington State Marine Water Quality in 1994 and 1995. Washington State Department of Ecology, Environmental Investigations and Laboratory Services Program, Publication #97-316, Olympia, WA.

Newton, J.A. and T.A. Morello. 1998. Phytoplankton growth and loss rates over the course of blooms in a temperate embayment. EOS, 79 (1): 141.

Officer, C.B. and J.H. Ryther. 1980. The possible importance of silicon in marine eutrophication. Marine Ecological Progress Series, 3: 83–91.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York.

Redfield, A.C., B.H. Ketchum, and F.A. Richards. 1963. The influence of organisms on the composition of sea-water. pp 26–77 in M.N. Hill [ed], The Sea, Vol. 2. Interscience.